

Resprouting vs seeding – a Mediterranean perspective

Juli G. Pausas, CEAM, C. Darwin 14, Parque Tecnológico, E-46980 Paterna, Valencia, Spain (juli@ceam.es).

In a recent paper, Bellingham and Sparrow (2000; B&S hereafter) proposed a model that predicts the relative importance of resprouting versus seeding in plant communities, on the basis of the disturbance regime (frequency and severity). The model suggests that seeding is more important at both low and high disturbance frequencies, while resprouting is favoured at the intermediate range. These predictions are in conflict with previous ones in fire-prone ecosystems, where seeder species are predicted to dominate at intermediate fire recurrence levels (e.g., Hilbert 1987, Lamont et al. 1991, Burgman and Lamont 1992). The B&S model was probably developed from the authors' experience in tropical ecosystems where events such as typhoons and hurricanes are important disturbance factors. Here I would like to point out several features of Mediterranean fire-prone ecosystems that I think should be taken into consideration before generalising the B&S model.

At high disturbance frequency, the B&S model predicts that seeding will be far more important than resprouting. Our experience in some fire-prone Mediterranean ecosystems (Pausas and Vallejo 1999) does not support this prediction. For example, in a large part of the eastern Iberian Peninsula, two tree species coexist: a pine that is not able to resprout (*Pinus halepensis*, Aleppo pine) and a resprouting oak (*Quercus ilex*, holm oak). The latter is less abundant due to its elimination in the past (e.g., past conversion from forest land to agricultural land, and now to old-fields; Pausas 1999a); furthermore, pines are planted by the Forest Service on old-fields. Despite this effort in pine plantation, sites with high fire recurrence are losing their pine, but not their oak populations. This is because the inter-fire interval in these places is shorter than the time that Aleppo pines need to produce viable seeds (15–20 yr) or to accumulate a critical seed store for self-replacement (Enright et al. 1998). If two consecutive fires

occur in less than 20 yr, the pine population of a region may be eliminated (see, for instance, van Wilgen 1981, Zedler et al. 1983, and Enright et al. 1996, 1998, for South African, Californian and Australian examples, respectively). Although high fire recurrence may reduce the capacity to resprout from fire (Vilà and Terradas 1995, Delitti et al. pers. comm.), most resprouting species will remain at the site (e.g., Traubad 1990) after consecutive fires.

Therefore, the hypothesis of the dominance by seeders at high levels of disturbance cannot be supported in fire-prone ecosystems without considering other life-history traits (e.g., Malanson 1985, Hilbert 1987, Pausas 1999b). For example, the large expanses of garrigue in the Mediterranean Basin are often located on high fire-recurrence areas where the shrub oak *Quercus coccifera* resprouts vigorously after recurrent fires (Malanson and Traubad 1988, Traubad 1990) or clipping (Tsiouvaras 1988), whereas pines are eliminated. In contrast, other seeder species, such as *Cistus* and *Ulex*, can be abundant if their age to maturity is less than an inter-fire period, or if their seed bank has not been exhausted by previous fires. A good example is the *Ulex* heathland in the eastern Iberian Peninsula, where the Mediterranean gorse, *Ulex parviflorus* (a non-sprouting species), is dominant. Such communities occur mainly on old-fields. The dominance of *Ulex parviflorus* in these heathlands is attributed to a) elimination of resprouting species in the past; b) maturity and seed production at a young age (2–3 yr); and c) production of a large soil seed bank, the dormancy of which is broken by the heat of a fire (Ballini 1992) or by other disturbance factors.

At the other extreme of the gradient, at low disturbance frequencies, the B&S model also predicts that seeding would be more important than resprouting. In the areas of the Iberian Peninsula where oaks have not been eliminated by humans, if fire is rare, the dominant

species is a resprouting oak (e.g., holm oak, *Quercus rotundifolia*). This is because holm oak is more shade-tolerant (Broncano et al. 1998) and shows higher longevity than Aleppo pine, and in the long term, holm oak displaces Aleppo pine in the absence of disturbance. The most striking example of the elimination of seeder species at a low disturbance frequency occurs in communities with non-resprouting species that have a high level of serotiny (i.e., fire-dependent seed release, with little inter-fire recruitment). In these cases, at long fire intervals which exceed the longevity of non-resprouters, these are eliminated whereas long-lived resprouters are not (Enright et al. 1998). High levels of serotiny are not observed in plants of the Mediterranean Basin but occur widely in other fire-prone ecosystems (Australia and South Africa). There is a wealth of information on the importance of fire for the recruitment of some disturbance-dependent seeders (e.g., Lamont et al. 1991, Burgman and Lamont 1992, Keeley 1995, Enright et al. 1996, 1998).

I believe that there is a need to consider several life traits simultaneously (such as age to maturity, shade tolerance, plant longevity, seed dormancy, serotiny), taking into account the work done in Mediterranean and other fire-prone ecosystems, before we can generalise any model for predicting the fitness of different reproductive strategies (seeding vs resprouting).

Acknowledgements – I thank B. Lamont and P. Bellingham for suggestions and corrections.

References

- Ballini, C. 1992. Écophysiologie de la germination des graines d'*Ulex parviflorus* Pourr. – Bull. Ecol. 23: 119–130.
- Bellingham, P. J. and Sparrow, A. D. 2000. Resprouting as a life history strategy in woody plant communities. – Oikos 89: 409–416.
- Broncano, M. J., Riba, M. and Retana, J. 1998. Seed germination and seedling performance of two Mediterranean tree species, holm oak (*Quercus ilex* L.) and Aleppo pine (*Pinus halepensis* Mill.): a multifactor experimental approach. – Plant Ecol. 138: 17–26.
- Burgman, M. A. and Lamont, B. B. 1992. A stochastic model for the viability of *Banksia cuneata* populations: environmental, demographic and genetic effects. – J. Appl. Ecol. 29: 719–727.
- Enright, N. J., Lamont, B. B. and Marsula, R. 1996. Canopy seed bank dynamics and optimum fire regime for the highly serotinous shrub, *Banksia hookeriana*. – J. Ecol. 84: 9–17.
- Enright, N. J., Marsula, R., Lamont, B. B. and Wissel, C. 1998. The ecological significance of canopy seed storage in fire-prone environments: a model for non-resprouting shrubs. – J. Ecol. 86: 946–959.
- Hilbert, D. W. 1987. A model of life history strategies of chaparral shrub in relation to fire frequency. – In: Tenhunen, J. D., Catarion, F. M., Lange, O. L. and Oechel, W. C. (eds), Plant response to stress. Functional analysis in Mediterranean ecosystems. Springer-Verlag, pp. 597–606.
- Keeley, J. E. 1995. Seed-germination patterns in fire-prone Mediterranean-climate regions. – In: Arroyo, M. T. K., Zedler, P. H. and Fox, M. D. (eds), Ecology and biogeography of Mediterranean ecosystems in Chile, California, and Australia. Springer-Verlag, pp. 239–273.
- Lamont, B. B., Le Maitre, D. C., Cowling, R. M. and Enright, N. J. 1991. Canopy seed storage in woody plants. – Bot. Rev. 57: 277–317.
- Malanson, G. P. 1985. Simulation of competition between alternative shrub life history strategies through recurrent fires. – Ecol. Model. 27: 271–283.
- Malanson, G. P. and Trabaud, L. 1988. Vigour of post-fire resprouting by *Quercus coccifera* L. – J. Ecol. 76: 351–365.
- Pausas, J. G. 1999a. Mediterranean vegetation dynamics: modelling problems and functional types. – Plant Ecol. 140: 27–39.
- Pausas, J. G. 1999b. The response of plant functional types to changes in the fire regime in Mediterranean ecosystems. A simulation approach. – J. Veg. Sci. 10: 717–722.
- Pausas, J. G. and Vallejo, V. R. 1999. The role of fire in European Mediterranean ecosystems. – In: Chuvieco, E. (ed.), Remote sensing of large wildfires in the European Mediterranean basin. Springer-Verlag, pp. 3–6.
- Trabaud, L. 1990. Fire resistance of *Quercus coccifera* L. garrigue. – In: Goldammer, J. G. and Jenkins, M. J. (eds), Fire in ecosystem dynamics. Mediterranean and northern perspectives. SPB Acad. Publ., pp. 21–32.
- Tsiouvaras, C. N. 1988. Long-term effects of clipping on production and vigor of kermes oak (*Quercus coccifera*). – For. Ecol. Manage. 24: 159–166.
- van Wilgen, B. W. 1981. Some effects of fire frequency on fynbos plant community composition and structure at Jonkershoek, Stellenbosch. – S. Afr. J. Bot. 118: 42–55.
- Vilà, M. and Terradas, J. 1995. Effects of competition and disturbance on the resprouting performance of the Mediterranean shrub *Erica multiflora* L. (Ericaceae). – Am. J. Bot. 82: 1241–1248.
- Zedler, P. H., Gautier, C. R. and McMaster, G. S. 1983. Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. – Ecology 64: 809–818.